

RELATIONSHIPS BETWEEN THE SEASONAL DYNAMICS OF SOIL FUNGI BIOMASS AND ENVIRONMENTAL FACTORS IN PREDOMINATING FOREST TYPES IN THE BRYANSK WOODLANDS (EUROPEAN RUSSIA)

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Being the crucial part of the forest soil's microbial pool, soil fungi in general and mycorrhizal fungi in particular are an important study object when it comes to forest ecosystems sustainability and preservation. Thus, the study of ectomycorrhizal fungi has been carried out in the Bryanskiy Les State Nature Biosphere Reserve, located in the south-eastern part of the Bryansk woodlands (European Russia). Forest types featured in the study are the local predominating types, namely green-moss-fructicolose pine forests and polydominant deciduous broadleaved nemoral-herbaceous forests with spruce. This study was aimed to assess seasonal dynamics of soil fungi' biomass overall and ectomycorrhizal fungi in particular over the course of the 2017 vegetation period (May – November) and its dependence on biotic and abiotic environmental factors, such as soil water content, temperature and vegetation. The vegetation period was divided into three periods of observation, namely an early (May – July), middle (July – September) and late (September – November) one. The method used to assess the fungal biomass was direct microscopic observation using the fluorescein diacetate staining. In order to estimate the ectomycorrhizal fungi biomass separately, trenching and in-growth mesh bags were employed. The obtained results suggest that the soil fungi biomass steadily increases over the vegetation period in both studied forest types. This is mostly affected by the forest type, available water amount and seasonal changes, while the temperature's impact is less pronounced. On average, the soil fungi biomass was higher in broadleaved forests than in pine forests (2.288 mg C × g⁻¹ soil vs. 1.672 mg C × g⁻¹ soil, respectively), with non-ectomycorrhizal component having comparable biomass. The dynamics of biomass differed in the two forest types. However, noticeable differences ($p < 0.1$) between the two forest types have only been recorded during the July – September period. The biomass of ectomycorrhizal fungi is smaller than the biomass of non-mycorrhizal fungi, but at the same time it is less affected by changes in moisture. Besides that, the study has shown that the forest litter characteristics can greatly affect the dynamics of the fungal biomass.

Key words: Bryanskiy Les State Nature Biosphere Reserve, deciduous-coniferous forests, ectomycorrhizal fungi, soil water, temperature, vegetation

Introduction

Forest ecosystems have a complex, multicomponent structure, one of the fundamental elements of which are soil fungi. They are the most important component of the forest soils microbial pools, constituting 60–80% of the forest soils' active biomass (Anderson & Domsch, 1975). Soil fungi, and especially mycorrhizal fungi, play a crucial role in the restoration and self-organisation of forest ecosystems (Futai et al., 2008). Inoculation with mycorrhizal fungi also improves plants vitality (Valdés et al., 2019) and may play a role in protecting them from diseases (Gonthier et al., 2019). The preservation of mycorrhizal fungal communities highly contributes to the stabilisation of forests and soils under negative impacts (Kropp & Langlois, 1990; Pagano, 2014).

The soil fungi are actively involved in the nutrient cycles, and mycorrhizal fungi are an integral part of the higher plant life, supplying the nutrients (Cairney, 2012; Bahr et al., 2013; Hendricks et al., 2016), and, according to some data, water as well (Allen, 2007) to plant symbionts. Mycorrhiza is the most important of the symbiosis involving plants and soil fungi. It is universal for most of the terrestrial ecosystems, since while non-mycorrhizal plants do exist, the non-mycorrhizal plant communities are virtually unheard of. The majority of plants form some type of the mycorrhiza (Brundrett, 2002). In the boreal zone, the main role belongs to ectomycorrhiza, associated with the woody plants dominating there. Mycorrhiza has a considerable impact on an ecosystem. Soil fungi are able to maintain communication between plants that belong

not only to various species, but also to various tiers, uniting them into a single system with a common circulation of biogenic elements (Read & Perez-Moreno, 2003; Booth, 2004). In addition, 50–70% of soil humus carbon enters from roots and fungi associated with them (Clemmensen et al., 2013), which makes mycorrhizal fungi one of the main sources of the stable soil carbon. The arbuscular mycorrhizal fungi contribute to the pool of stable soil organic matter by increasing the amount of mineral-associated organic matter in the lower soil horizons (Craig et al., 2018; Keller et al., 2021), while the ectomycorrhizal fungi produce more recalcitrant organic matter in the upper horizons that takes longer to decompose (Cornelissen et al., 2001; Clemmensen et al., 2013; Craig et al., 2018). This makes mycorrhizal fungi overall a very important factor of climate regulation.

Many studies show that the biomass and composition of soil fungi communities in forests can depend on external factors such as temperature, humidity, soil type, nutrient content and vegetation composition and structure (Wallander et al., 2001; Pietikäinen et al., 2005; Kaisermann et al., 2015; Štursová et al., 2020; Karliński, 2021). However, the nature of this dependence and quantitative indicators vary highly in various studies, with authors coming to opposite conclusions about just how the soil fungi are affected by seasonal changes in environment (Okada et al., 2011; Štursová et al., 2020). Moreover, it was shown that certain factors, while not necessarily affecting the biomass of fungi, can cause shifts in the fungal communities' composition (Kaisermann et al., 2015). Finally, such studies are still fairly few and far between in Russia. Most of them have been conducted on abandoned arable lands (Susyan et al., 2011; Nikitin et al., 2019) or in different climate zones (Korneykova et al., 2023).

Meanwhile, with the climate is changing, the understanding of the processes occurring in forest soils under the influence of these conditions can be crucial in conservation efforts and sustainable management of the forest ecosystems. Forest conservation and degradation mitigation, as well as sustainable forest management are important strategies for maintaining ecosystem resilience. All of them may highly benefit from studying the conditions, under which soil fungi function in forest ecosystems (Simard & Austin, 2010).

In this regard, the aim of this study was to assess the impact of biotic (forest type) and abiotic (temperature and moisture conditions) environmental factors on the soil fungi biomass seasonal dynamics

in the dominant types of coniferous-deciduous forests in Eastern Europe, in the Bryanskiy Les State Nature Reserve, European Russia. The main scientific question answered by this article is what factors can explain the seasonal dynamics of soil fungi biomass?

Material and Methods

Study area

The study plots were set up in the Bryanskiy Les State Nature Biosphere Reserve (European Russia), within the coniferous-deciduous mixed forests zone (Fig. 1). The local climate is temperate continental. The average temperature is -7°C to -9°C in January, and 18 – 19°C in July. The average annual precipitation in the study area (Bryanskiy Les State Nature Biosphere Reserve) is 560–600 mm (Kuznetsova et al., 2019).

In order to assess the seasonal dynamics of the soil fungi and the environmental factors affecting them, four study plots were established in two forest types, two in each, namely green-moss-fructulose pine forests (hereinafter – pine forests) and polydominant deciduous broadleaved nemoral-herbaceous forests with spruce, *Picea abies* (L.) H.Karst. (hereinafter – broadleaved forests) (Fig. 2). Broadleaved forests are considered secondary forests in the study area, situating on the previously disturbed areas, being recognised as the most common forest type there. Their cover percentage is 70–90%. Broadleaved forests represent an advanced stage in the vegetation formation in absence of any major anthropogenic impacts for a long time (e.g. more than 120 years) (Gornov et al., 2018). The factors considered in this study were vegetation (including litter quality), soil temperature and gravitational water amount.

Soil characteristics

The on-site studies have been carried out in 2016–2017. They showed that the soil cover is dominated by Albic Umbric Podzol (IUSS Working Group WRB, 2015) on fluvio-glacial sediments. The soil has a light texture, with 1.2–1.3% of a heavy (< 0.002 mm) fraction. In pine forests, the upper, destructive layer of the forest litter (L horizon) consists of the past and current year litter (*Pinus sylvestris* L. needles, leaves of *Quercus robur* L., bark, pine cones, and small twigs) and dead moss with the predominance of *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Dicranum polysetum* Sw. The thickness of pine forest's litter is 3–7 cm. In broadleaved forests, horizon L is characterised by an abundance of leafy litter consisting of *Acer*

platanoides L., *Ulmus glabra* Huds., *Tilia cordata* Mill., *Betula pubescens* Ehrh., and *Q. robur*. Numerous acorns, tree bark and twigs can also be found in the litter. The lower, fermentative-humified, layer of the forest litter (FH horizon) mostly contains decaying litter and wood residues. It is permeated with numerous plant roots and mycelium. The litter in broadleaved forests differs from the one in pine forests by being thinner (2–4 cm) and having a higher fragmentation rate of the enzymatic horizon. It happens due to the rapid mineralisation of leafy litter and its integration in an active biological cycle (Kazakova et al., 2018). The details on soil features can be found in Table 1.

Vegetation characteristics

In the geobotanical studies, 20 × 20-m plots were laid out in 2017. In total, 11 descriptions

were made in pine forests and 13 in broadleaved forests, due to its more complex structure. The complete floristic list has been compiled for all sites, taking into account the layered structure of the forest. In each stage, the projective coverage of plant species was assessed according to Braun-Blanquet (1964). Scientific names of vascular plants are given according to the Plants of the World Online database (<https://powo.science.kew.org/>). To assess seasonal changes in vegetation cover, data from the permanent phenological route of the Bryanskiy Les State Nature Biosphere Reserve were used. Observations began from the time of stable transition of the maximum air temperatures through the zero mark. The monitoring frequency of the plant development was once every five days, and the woody plants' stages of development were taken into account.

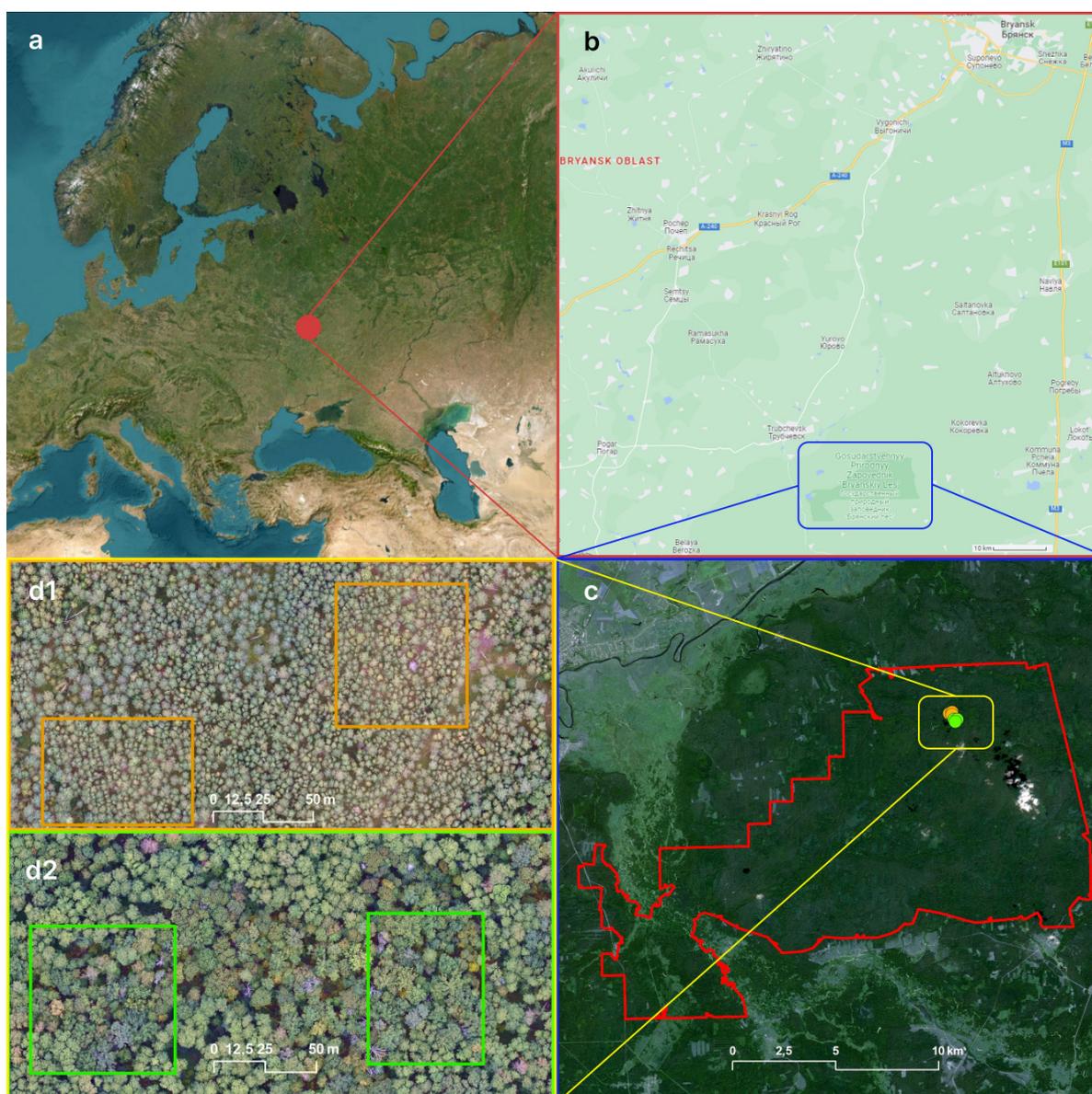


Fig. 1. The location of the Bryanskiy Les State Nature Biosphere Reserve (a, b) and the study plots (c; d1 – pine forests; d2 – broadleaved forests).

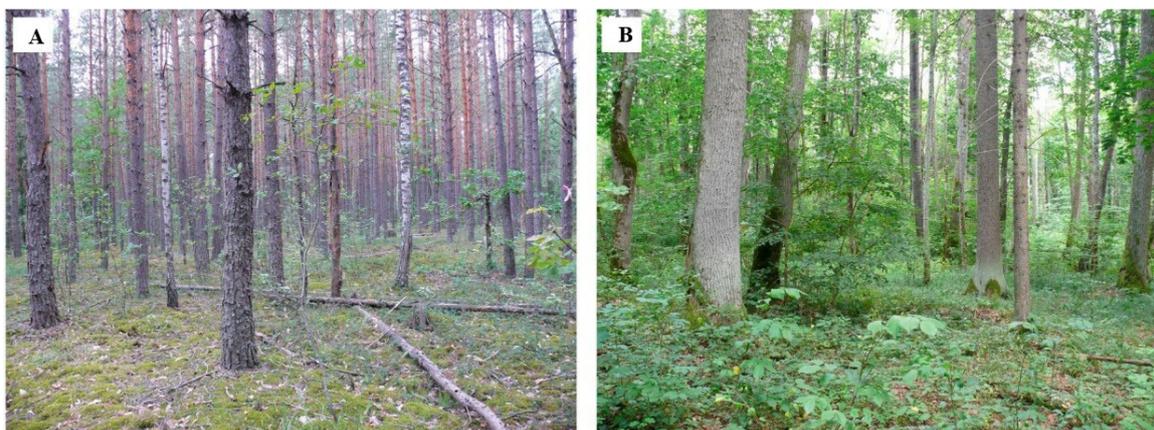


Fig. 2. The pine forest (A) and broadleaved forest (B) presented on the study plots in the Bryanskiy Les State Nature Biosphere Reserve, Russia.

Table 1. Studied forest types’ soil and vegetation characteristics on both study plots in the Bryanskiy Les State Nature Biosphere Reserve in 2016–2017

Forest type	Pine forests	Broadleaved forests
Soil characteristics		
Litter store, kg × m ²	2.5 ± 0.2	1.3 ± 0.1
Litter pH	4.7 ± 0.4	6.1 ± 0.3
Litter C/N ratio	34 ± 7	21 ± 4
Litter N, %	1.4 ± 0.3	2.0 ± 0.2
Horizon AY C/N	18 ± 2	11 ± 1
Horizon AY N, %	0.08 ± 0.01	0.23 ± 0.03
Vegetation characteristics		
Forest stand’s composition	90% <i>Pinus sylvestris</i> , 10% <i>Betula pubescens</i> + solitary <i>Quercus robur</i>	30% <i>Quercus robur</i> , 30% <i>Acer platanoides</i> , 30% <i>Tilia cordata</i> , 10% <i>Picea abies</i> + solitary <i>Ulmus glabra</i> , <i>Populus tremula</i> , and <i>Fraxinus excelsior</i>
Forest stand’s age, years	40–60	> 120
Number of studied plots	11	13
Storey A, %	58.64 ± 1.66	72.08 ± 5.79
Storey B, %	22.45 ± 5.57	35.83 ± 3.53
Storey C, %	46.82 ± 3.77	68.33 ± 2.61
Mean number of species:	14	34
Storey A	1.64 ± 0.15	5.33 ± 0.26
Storey B	3.91 ± 0.21	5.33 ± 0.36
Storey C	12.45 ± 0.78	32.25 ± 0.27

Pine forests are formed by the predominant *Pinus sylvestris*, sometimes with participation of *Betula pubescens*, and solitary *Quercus robur*. The undergrowth layer consists of *B. pubescens*, *Q. robur*, and *Picea abies*. Among shrubs, *Frangula alnus* Mill. and *Chamaecytisus ruthenicus* (Fisch. ex Woł.) Klásk. have been recorded. The herb cover was dominated by boreal species, namely *Vaccinium vitis-idaea* L., *V. myrtillus* L., *Calluna vulgaris* (L.) Hull. The green-moss coverage was high, reaching 90%.

In broadleaved forests, the tree layer is dominated by *Quercus robur*, *Picea abies*, *Acer platanoides*, *Tilia cordata*, *Ulmus glabra*, and *Fraxinus excelsior* L. The undergrowth layer was dominated by *U. glabra*, *A. platanoides*, *T. cordata*, while such species as *P. abies* and *F. excelsior* were less common. Shrubs were mostly represented by *Corylus avellana* L. and *Prunus padus* L. The herb cover was dominated

by nemoral plants, namely *Rabelera holostea* (L.) M.T.Sharples & E.A.Tripp., *Carex pilosa* Scop., *Mercurialis perennis* L., and *Aegopodium podagraria* L. Ground bryophytes did not seem to grow in these forests due to the scarcity of light resource. Further details on forest layers can be found in Table 1.

Soil fungi study

When assessing the soil fungi biomass dynamics in both forest types, four 1 × 2-m study plots were established in 2016. Two plots were selected as «natural» without any special treatments. The other two plots (isolated control) were entrenched and isolated from the surrounding soil by sheets of 2 mm thick foamed polyvinyl chloride (PVC) plastic up to 1 m in depth. This was done to isolate the study area from the root systems of trees, and thus, to exclude the ectomycorrhizal fungi (Fisher & Gosz,

1986). The sheet joints at the corners of the plots were additionally reinforced using polyethylene film. After laying down the isolation and burying it from the outside, the plots were left for a year for incubation, which resulted in the chopped tree roots dying out and the cessation of mycorrhizal relations on the isolated plots. In pine forests, all shrubs were also removed from the experimental plots.

On the «natural» plots, the mycelium biomass assessment for all the functional groups of soil fungi was carried out in samples taken from the top 10-cm soil layer. The exact method was as follows: five smaller samples were collected in the corners and the centre of a square plot of 1 m² and then combined into one mixed sample.

To assess specifically the biomass of mycorrhizal mycelium, batches of mesh bags were prepared: 24 rectangular bags of polyamide mesh fabric (5 × 10 × 2 cm; 56-µm mesh diameter). The bags were filled with washed quartz sand (grain diameter: 0.5–1.0 mm) and then sealed. Afterwards, three bags were placed on all sites. The placement was vertical, covering the depth of 0–10 cm under the litter (i.e. the most root-inhabited soil layer). The bags were exposed for two months, starting from May, after which the bags were removed, and the next batch was laid in their place. In total, three batches of 24 bags were laid by this way, making up three periods of exposure, namely May – July, July – September, and September – November 2017. Thus, they cover the vegetation season in the Bryanskiy Les State Nature Biosphere Reserve. The design was chosen based on the studies showed that the vast majority of fungal mycelium biomass growing into sacs is ectomycorrhizal (Wallander et al., 2001). However, the method requires a control batch as well in order to take into account a possible error, since Boddy (1993) shows the ability of rhizomorphic fungi to grow in areas with extremely low nutrient concentrations. Nilsson et al. (2005) mentioned arbuscular mycorrhizal fungi mycelium growing into the bags under certain circumstances, while Carteron et al. (2021) confirmed that the mycelium of the saprotrophic fungi can still be found there, despite the absolute predominance of mycorrhizal fungi in low-nutrient mineral soil horizons. Thus, the bags were placed on the isolated sites as a control, showing the possible error of the method.

The biomass of mycorrhizal mycelium was determined by the difference between the average biomass of the mycelium in the mesh bags on the «natural» and isolated plots. The biomass of non-mycorrhizal mycelium was determined by the

difference between the biomass of mycelium in soil samples taken from the «natural» plots and the biomass of mycelium from the mesh bags from the «natural» plots.

The exact method was as follows: an aqueous suspension of sand from the mesh bags/soil samples (sand samples: 10 ml of distilled water, 2.5 g of sand; soil samples: 100 ml of distilled water, 1 g of soil) was stirred on a vortex (Biosan V1 plus) for 1 min., after which 5 ml of the supernatant was filtered through a Whatman polycarbonate membrane (hole diameter: 0.4 µm). For determining the fungi biomass, the luminescent staining method was chosen as an often employed, reliable and easily accessible method (Korneykova et al., 2022; Nikitin et al., 2023). The membranes were then stained with fluorescein diacetate (Söderström, 1977). Then, the membranes were examined under a fluorescent microscope at × 40 magnification with 30 fields of view per sample. The stained hyphae of fungi were measured using an eyepiece with a ruler. Then, the length of the hyphae was re-calculated into their mass using the formula proposed by Zvyagintsev (1991). The data obtained were used to calculate the dynamics of the biomass of soil fungi during the growing season.

Soil water and temperature

An assessment of the abiotic factors was conducted as a part of complex biogeocenotic studies in the study area, employing rain catchers, lysimeters, and Thermochron iButton temperature loggers. In order to characterise the temperature regime of the studied periods (vegetation period of 2017), three loggers have been placed in both forest type, right underneath the LFH horizons (5 cm). For each period, the mean temperature and the sum of active temperatures (exceeding 10°C) have been calculated. As for the assessment of the water supply for the studied periods, ten rain catchers and six soil lysimeters (as designed by Derome & Nieminen (1998) placed underneath the LFH horizons at 5-cm deep) have been placed in the under-crown areas in both forest types, six rain catchers and three lysimeters in each. Accounting for the volume of throughfall (i.e. precipitation coming through the forest canopy to the ground) and soil water volumes assessment was carried out monthly.

Statistical analysis

Statistical processing of the results was carried out in the STATISTICA 12.0 (StatSoft, Germany; <https://www.statsoft.de/en/home/>)

package ($\alpha = 0.05$). The significance of differences was assessed using the Mann-Whitney U-test. To assess the dependence between the biomass of various groups of soil fungi and environmental conditions, a selection of essential features was compiled based on the study of correlations between the abiotic (temperature, precipitation and gravitational soil water content) environmental factors and the biomass of soil fungi. In order to assess the degree of influence of environmental conditions on the state of various groups of soil fungi, the Spearman correlation coefficients were calculated for the biomass value and the values of other studied factors.

Results

Seasonal dynamics of the soil fungi

The soil fungi biomass has been found steadily increasing throughout the vegetation period from 1.127 mg C × g⁻¹ soil in May – July to 2.587 mg C × g⁻¹ soil in September – November in pine forests ($p < 0.05$) (Table 2). In broadleaved forests, the results were less obvious ($p < 0.1$). In their case, the absolute minimum occurred during the May – July period as well (1.040 mg C × g⁻¹ soil). However, the maximum was registered during the July – September period (3.600 mg C × g⁻¹ soil).

The biomass of non-ectomycorrhizal fungi throughout the growing season in pine forests varied from 0.771 mg C × g⁻¹ to 2.120 mg C × g⁻¹ (Table

2). The biomass of ectomycorrhizal mycelium (EM) in soils ranged from 0.233 mg C × g⁻¹ to 0.467 mg C × g⁻¹. During the autumn (September – November) period, the biomass of both EM and non-ectomycorrhizal mycelium (non-EM) was on average higher than in the summer (May – September) period, but the distinction was non-significant ($p < 0.1$). In pine forests, the ratio of EM to non-EM significantly ($p < 0.05$) shifted towards the non-EM (up to 1:5), reaching a maximum in the autumn period.

In broadleaved forests, the biomass of non-EM was in the range of 0.639–2.691 mg C × g⁻¹ (Table 2). The lowest biomass was recorded in the period from May to June, while the highest one in the period from July to September ($p < 0.1$). The biomass of EM in soils was relatively constant and ranged from 0.400 mg C × g⁻¹ to 0.909 mg C × g⁻¹. In broadleaved forests, the ratio of EM to non-EM was less skewed towards the non-EM fungi, reaching 1:3 in the July – September period.

On average, the soil fungi biomass was higher in broadleaved forests at 2.288 mg C × g⁻¹ soil, compared to pine forests (1.672 mg C × g⁻¹ soil). It is worth mentioning though, that over the course of the vegetation period the fungal biomass was comparable in both forest types most of the time. However, the July – September period demonstrated a dramatic increase the biomass of soil fungi in broadleaved forests.

Table 2. Seasonal dynamics of the soil fungi biomass and the abiotic environmental factors measured in the Bryanskiy Les State Nature Biosphere Reserve during the vegetation period in 2017

Indicators	Time period					
	01.05 – 01.07		01.07 – 01.09		01.09 – 01.11	
	M	SD	M	SD	M	SD
Pine forests						
Fungal biomass, mg C × g ⁻¹ soil comprising:	1.127	0.199	1.301	0.417	2.587	0.755
EM	0.356	0.065	0.233	0.105	0.467	0.079
Non-EM	0.771	0.264	1.068	0.312	2.120	0.675
Precipitation amount, mm	54.787	15.371	143.810	4.222	71.656	0.704
Lysimetric water amount, mm	6.513	1.567	16.799	0.338	27.070	22.519
Temperature, °C	11.7	2.1	16.1	1.4	11.4	2.8
Sum of active temperatures (> 10°C)	526.2	–	998.5	–	535.4	–
Broadleaved forests						
Fungal biomass, mg C × g ⁻¹ soil comprising:	1.040	0.034	3.600	0.120	2.224	0.683
EM	0.400	0.056	0.909	0.606	0.777	0.146
Non-EM	0.639	0.023	2.691	0.726	1.447	0.214
Precipitation amount, mm	50.590	7.506	150.527	5.278	70.910	13.723
Lysimetric water amount, mm	0.0	–	11.2	11.3	4.5	0.1
Temperature, °C	12.4	2.6	16.6	2.1	10.4	3.5
Sum of active temperatures (> 10°C)	553.8	–	1030.0	–	381.1	–

Note: M – mean value, SD – standard deviation, EM – ectomycorrhizal mycelium, Non-EM – non-ectomycorrhizal mycelium.

The non-EM biomass was generally comparable in both pine and broadleaved forests and amounted on average to 1.320 mg C × g⁻¹ and 1.592 mg C × g⁻¹, respectively. However, when comparing seasonal dynamics, some differences can still be observed. In the periods of May – July and September – November, the biomass of non-EM was higher in pine forests (on average 0.771 mg C × g⁻¹ and 2.120 mg C × g⁻¹, respectively) than in broadleaved forests (0.639 mg C × g⁻¹ and 1.447 mg C × g⁻¹, respectively). On the contrary, in the period of July – September, the biomass of non-EM was higher in broadleaved forests (on average 2.691 mg C × g⁻¹) compared to pine forests (1.068 mg C × g⁻¹).

The biomass of EM on average was higher in broadleaved forests than in pine forests and amounted to 0.695 mg C × g⁻¹ and 0.352 mg C × g⁻¹, respectively. In the period of May – September, the biomass of EM tended to be higher (p < 0.1) in broadleaved forests. The biomass of non-EM fungi in both forest types was generally higher than the biomass of EM fungi. The growth dynamics of non-EM fungi turned out to be different in pine forests and broadleaved forests. In pine forests, its maximum occurs in November, while in broadleaved forests in September.

Seasonal dynamics explains 52% of the EM biomass dispersion (p < 0.1) and 73% of the non-EM biomass (p < 0.05). The periods with different moisture levels explain 66% of fungal biomass

(p < 0.05), mostly due to the contribution of the non-EM fungi (Table 3).

Temperature

In pine forests (Table 2), the sum of active temperatures (exceeding 10°C) was 2060°C for the observation period, which is comparable to broadleaved forests, where the sum of active temperatures was 1965°C. The average temperature of the organogenic soil horizons in both forest types was 13.1°C, with both forests having the coldest period in September–November (11.4°C and 10.4°C respectively) and the warmest in July – September (16.1°C and 16.6°C). Among the three studied periods, the one in autumn (September – November) had the highest difference in temperatures between the two forest types. Being the coldest period, this difference bore extra significance for the plants and soil organisms alike. The autumn period was solely the reason the total sum of active temperatures turned out to be higher in pine forests.

The amplitude of soil temperature changes at various times of the day (daily dynamics) was smaller in pine forests compared to broadleaved forests (Fig. 3). Thus, it can be stated that the temperature fluctuations were milder in soils in pine forests than in soils in broadleaved forests. These differences can be explained by differences in the tree layer composition, which leads to differences in the litter thickness in the studied areas (2–4 cm in broadleaved forests vs. 3–7 cm in pine forests).

Table 3. One-way ANOVA of various factors, affecting temperature, throughfall, soil lysimetric water volumes and soil fungi in the Bryanskiy Les State Nature Biosphere Reserve (Russia) during the vegetation period of 2017

Variables	Factor										
	Forest type		Seasonal dynamics (summer – autumn periods)				Moisture-driven dynamics (dry – moist periods)				n
			Pine forests		Broadleaved forests		Pine forests		Broadleaved forests		
	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p	
Temperature											
Temperature, °C	0.01	0.951	0.31	0.255	0.56	0.086	0.20	0.375	0.04	0.707	6
Sum of active temperatures (> 10 °C)	0.01	0.844	0.24	0.329	0.49	0.117	0.26	0.296	0.07	0.618	6
Throughfall and soil lysimetric water volumes											
Throughfall, mm	0.01	0.982	0.11	0.518	0.10	0.536	0.41	0.173	0.42	0.162	20
Lysimetric water amount, mm	0.09	0.253	0.34	0.224	0.01	0.887	0.34	0.224	0.32	0.237	10
Soil fungi											
Fungal biomass, mg C × g ⁻¹ soil	0.09	0.319	0.76	0.025	0.01	0.937	0.27	0.293	0.66	0.048	12
EM	0.19	0.159	0.52	0.106	0.01	0.825	0.01	0.962	0.18	0.402	12
Non-EM	0.02	0.596	0.73	0.030	0.01	0.829	0.34	0.222	0.56	0.086	12

Note: R² – coefficient of determination, p – p-value, EM – ectomycorrhizal mycelium, Non-EM – non-ectomycorrhizal mycelium.

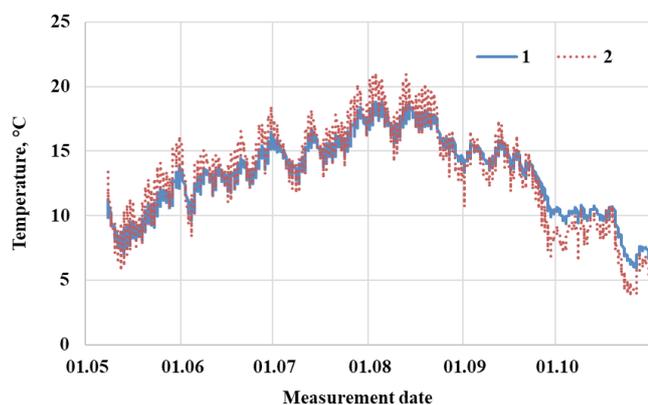


Fig. 3. Daily amplitude of the temperature of the organogenic horizons in pine forests (1), and broadleaved forests (2) in the Bryanskiy Les State Nature Biosphere Reserve, Russia.

During the first two studied periods (May – July and July – September), the average temperatures and the sum of active temperatures were rising steadily, followed by a sharp decline at the end of the second period or beginning of the third period (September – November). These dynamics were observed in both forest types. Seasonal dynamics explain 43% of the average temperature dispersion ($p < 0.05$) and 36% of the active temperature sum dispersion (Table 3).

Water regime

In general, the vegetative season started with a period of draught, with the largest amount of precipitation coming between July and September. This period is also distinguished by the highest average temperature. Comparing the beginning of the summer period (May – June; hereinafter – dry period) with the later, moister summer and autumn transitional period (July – October; hereinafter – moist period), a significant ($p < 0.01$) increase in the amount of precipitation coming under the forest canopy was revealed and, accordingly, the increased volume of lysimetric waters ($p < 0.1$). Periods with different moisture levels explain 41% of the throughfall dispersion ($p < 0.05$) and 23% of the lysimetric waters volumes ($p < 0.1$) (Table 3).

In pine forests, the throughfall amount was 270 mm for the observation period. The amount of free soil water in lysimeters was 51 mm. The wettest period lasted from July to September. The highest amount of soil water was recorded in the autumn period (September – November) (Table 2).

In broadleaved forests, the throughfall amount was 272 mm. The amount of free soil water in lysimeters was 16 mm. The wettest period lasted from July to August. The highest

amount of soil water was recorded from July to September. From May to July, no soil water runoff was recorded, which indicates extremely dry conditions during this period.

After assessing the moisture conditions in both forest types, the amount of lysimetric waters in broadleaved forests was found to be significantly ($p < 0.05$) lower, compared to pine forests. Thus, the water availability can be considered the main limiting factor in broadleaved forests. In pine forests, it is also crucial to take into account the soils' temperature regime, as they may affect the ectomycorrhizal fungi biomass and the group composition of soil fungi overall.

Despite the close proximity of the studied sites, the environmental conditions in their soils had noticeable differences. A thicker litter in pine forests (Table 1) retained moisture better than the litter in broadleaved forests. An accumulation of moisture was observed in pine forests towards the end of the growing season. Unlike pine forests, broadleaved forests went through the periods with zero lysimetric water volume, and the volume of gravitational water directly correlated with the amount of precipitation during the corresponding period. To sum up, both the temperature and moisture conditions in pine forests' soils were more stable throughout both a day and a year, forming a milder climatic regime than the one in soils in broadleaved forests.

Vegetation

Noticeable differences were found between pine and broadleaved forests in terms of floristic composition, stem wood stock, projective cover of forest layers, and species richness. The highest species richness was recorded in broadleaved-spruce forests (34 species), while in pine forests it was noticeably lower (14 species).

The one-way ANOVA test shows the lack of the «forest type» factor's contribution to the considered indicators' variation (Table 3). However, the vegetation itself was shown to have an indirect effect, taking into account the seasonality of samples. The «seasonal dynamics» factor had noticeable value for most of the indicators, both within each forest type and when comparing them to each other (Table 3). Clear seasonal dynamics were observed based on the phenological observations of woody plants carried out in 2017 (Table 4).

Table 4. Projective plant cover and phenological observations of woody plants in the Bryanskiy Les State Nature Biosphere Reserve (Russia) in 2017

Species (n)	Projective plant cover, %		Leaves sprouting, beginning	Full leaves sprouting	Mass ripening/falling of fruits	Autumn colouration, beginning	Mass autumn colouration	Leaves fall, beginning	Mass leaves fall	Leaves fall, end
	Pine forests	Broadleaved forests								
<i>Betula pubescens</i> Ehrh.	10	10	27.04	13.05	–	15.09	10.10	21.09	13.10	21.10
<i>Quercus robur</i> L.	5	35	03.05	05.06	–	16.09	09.10	24.09	16.10	23.10
<i>Acer platanoides</i> L.	1	25	–	14.05	–	18.09	24.09	22.09	07.10	11.10
<i>Tilia cordata</i> Mill.	–	20	–	–	–	14.08	27.09	–	06.10	14.10
<i>Prunus padus</i> L.	–	5	–	10.05	–	–	–	28.08	10.09	10.10
<i>Frangula alnus</i> Mill.	20	5	–	–	05.08	08.08	–	09.09	25.09	20.10
<i>Corylus avellana</i> L.	–	5	–	–	–	25.09	10.10	05.10	13.10	20.10

The active leaf fall period starts in September and lasts till late October. This coincides with the last, autumn, period. In pine forests, the projective plant cover is noticeably smaller than in broadleaved forests (Table 1). Therefore, the litter amount in pine forests is also comparatively lower, which can be considered an additional limiting factor for the soil fungi in pine forests' soils.

Assessing the environmental condition effects on soil fungi

The obtained data allow us to trace certain relationships between the biomass of various soil fungi groups and environmental conditions. It has been established that the biomass of ectomycorrhizal mycelium in pine forests is more affected by the temperature regime. It is characterised by a highest correlation index (Table

5). At the same time, the ratio of EM to non-EM in pine forests was influenced by the amount of precipitation and soil water, as well as the sum of active temperatures over 10°C. In broadleaved forests, no linear relationships with abiotic factors were found for the EM fungi.

Thus, it can be stated that the EM fungi biomass is affected by the temperature regime, which manifested itself in pine forests with more moisture. At the same time, in relatively dry broadleaved forests, this pattern did not show itself so evidently, and changes in the EM fungi biomass were generally multidirectional.

Considering the non-EM biomass in broadleaved forests, the relationships can be most clearly traced with the amount of lysimetric water and the amount of atmospheric precipitation. In pine forests, no linear relationships with abiotic factors were found for the non-EM.

Table 5. Spearman correlation (R_s) of soil fungi biomass with various environmental conditions on study sites in the Bryanskiy Les State Nature Biosphere Reserve (Russia) in 2017

Parameters	Temperature, °C	Sum of active temperatures (> 10°C)	Throughfall, mm	Lysimetric water amount, mm
Pine forests				
EM fungal biomass	-0.96***	-0.48	-0.48	0.14
Non-EM fungal biomass	-0.60	0.24	0.31	0.60
Proportion of the EM fungi from total biomass	-0.24	-0.84**	-0.71*	-0.77*
Broadleaved forests				
EM fungal biomass	0.24	0.24	0.31	0.12
Non-EM fungal biomass	0.48	0.48	0.94***	0.81**
Share of the EM fungi from total biomass	-0.12	-0.12	-0.37	-0.49

Note: EM – ectomycorrhizal mycelium, Non-EM – non-ectomycorrhizal mycelium, R_s – Spearman's rank correlation coefficient; asterisks (*) indicate the correlations' significance: * – $p \leq 0.1$, ** – $p \leq 0.05$, *** – $p \leq 0.01$.

Thus, the direct influence of the forest (formation of various symbiotic relationships between various species of dominant woody plants with local soil fungi), and the indirect influence (changes in local conditions of the soil fungi functioning, such as the temperature regime of soils, soil moisture and water supply) lead to changes in the biomass and group composition of soil fungi. Each forest type brings forth a corresponding set of abiotic factors affecting the soil and soil fungi.

Discussion

Effect of the temperature on the soil fungi biomass

The temperature regime is widely considered one of the leading factors that can affect the biomass production and the activity of soil fungi (Compant et al., 2010; Okada et al., 2011; Osono et al., 2011). Osono et al. (2011) showed that the rate of growth and decomposition of the substrate by fungi directly depend on temperature, with a clearly pronounced maximum when thermal optimums are reached and a decrease in activity when moving away from them. Pietikäinen et al. (2005) show that soil respiration increases with temperature, reaching a peak when a certain limit is reached. Compant et al. (2010) stated the decrease in the EM fungi' biological activity as one of the consequences of an increase in temperature. For pine forests, there was recorded an inverse relationship between the dynamics of fungal biomass and temperature (Okada et al., 2011). This is also confirmed by our data, since the absence of a significant increase in the production of fungal mycelium was recorded in the warmest period (Table 2). However, Okada et al. (2011) also noted the variability of such trends in various years, so there may be more factors affecting the outcome.

In contrast to pine forests, in broadleaved forests a decrease in the biomass of soil fungi can be found in the period from September to November, where the average temperature decreases, and the highest amplitude of daily temperatures was observed (Fig. 4). In natural forest ecosystems, differences in vegetation and litter can explain the difference in daily temperature dynamics. The litter thickness is higher in pine forests, which provides the underlying soil with better insulation. This leads to a smaller amplitude of daily changes in soil temperature and higher soil temperatures in the colder autumn period, compared to broadleaved forests with thinner and relatively less developed litter layer (Table 1). Temperature fluctuations were mentioned as one of the factors with an adverse impact on biological processes (Xu, 1996).

Influence of the throughfall and lysimetric water volumes on the soil fungi biomass

According to Heinemeyer et al. (2007), Allison & Treseder (2008), Compant et al. (2010), and Hawkes et al. (2011), low soil moisture can be a limiting factor for the soil fungi's vital activity. Since the amount of soil water in pine forests, even in the driest part of the growing season, was 1.5–2.0 times higher than in the wettest season in broadleaved forests, where the biomass of soil fungi was comparable to that in pine forests, it can be assumed that the humidity was not the limiting factor for at least the pine forests' soil fungi.

The growth dynamics of the non-EM fungi was found to be closely related to the soil moisture, since in pine forests the peak of non-EM fungi biomass occurs in September – November, and in July – September in broadleaved forests. It coincides with the humidity peak, i.e. the highest amount of soil water in both forest types. In both forest types, the minimum biomass was recorded in the period from May to July, which coincides with the driest conditions in soils during the vegetation season.

During periods of lower rainfall (May – July and September – November), the biomass of non-EM fungi was higher in pine forests compared to broadleaved forests. Such a difference can be explained by the higher moisture content of pine forest soils, where a higher amount of soil water was recorded during these periods in comparison with broadleaved forests, by creating more comfortable conditions for a longer time for saprotroph organisms, which are unable to directly receive the required water from plant symbionts.

In predominantly oak forests of the temperate zone, the pre-existing data on the biomass dynamics of EM fungi also indicated an increase in the EM fungi biomass at late summer and its subsequent decrease by late autumn (Voříšková et al., 2014). In general, in broadleaved forests, the soil fungi's biomass dynamics curve has a very typical shape, with a maximum at late summer, and a minimum at early summer, which corresponds to the literature (Wallander et al., 2001; Allen & Kitajima, 2014; Voříšková et al., 2014; Štursová et al., 2020).

Influence of vegetation on the soil fungi biomass

Vegetation indirectly affects the production of fungal biomass, for instance, by changing the temperature and water regime (Laganière et al., 2012; Wang et al., 2019). The litter thickness and quality seem to have a major impact on the upper organogenic soil horizons' temperature regime. According to our data, the litter thickness and its stock determine the fluctuation amplitude for the temperature regime of

the organogenic horizon. The water regime of the upper organogenic soil horizons depends on both the throughfall amount, regulated mainly by the forest canopy, and the litter properties. With almost the same amount of precipitation, the amount of free soil water in both forest types differed significantly (Table 2), which is associated with different activity of water absorption by vegetation (Lukina, 2018) and different water interception and absorption capacity in the litter of pine and broadleaved forests (Sato et al., 2004). Moreover, by the virtue of being a supplier of organic material, vegetation also affects the production of fungal biomass directly through the quantity and quality of litter on the one hand, and through the ability to form symbiotic bonds on the other hand (Kernaghan, 2005).

The growth dynamics of non-mycorrhizal fungi turned out to be different in pine and broadleaved forests. In case of pine forests, the maximum occurs in the period of September – November, while in broadleaved forests, it occurs in the period of July – September. In pine forests, due to the insignificant amount of easily decomposable litter, fungal communities may demonstrate a more pronounced reaction to its input. The peak of the non-EM fungi biomass coincides with the humidity peak, as well as with the influx of the main proportion of *Betula pubescens* litter. Autumn litter seems to be the most intensively concentrated influx of relatively easily decomposable material in local pine forests, which contributed to an increase in the biomass of saprotroph organisms under conditions of sufficient moisture. In general, the relationship between the vegetative activity of plants and the dynamics of fungal biomass can also be affected by the EM fungi symbiosis in soils (Smith & Read, 2008).

In broadleaved forests, there is a sufficient amount of nutrient substrate for the saprotrophic fungi, since the litter of deciduous trees and herbs is rich in easily decomposable compounds. Therefore, when water regime conditions become optimal, a high production of non-EM fungi could be observed there. It should also be noted, that from September to November, when the litter amount was much higher, the biomass of non-EM fungi decreased significantly (almost two-times decrease), which coincides with an almost two-fold decrease in the soil water volume. In this case, humidity seems to be a more significantly limiting factor.

In both forest types, the biomass of EM fungi in the period from May to July, characterised by a low amount of precipitation and soil water, was almost the same. Perhaps this is caused by the fact that

this was the least favourable period for the biomass production due to the lack of water and a low amount of incoming forest litter during the period. Because EM fungi can obtain water from the plant, they may not depend much on the upper soil layer's moisture by surviving this period in a relatively stable state (Smith & Read, 2008).

Smith & Read (2008) also mentioned that a higher plant species richness leads to a higher diversity and biomass of mycorrhizal symbionts, which occurred in our study during the periods of July – September and September – November. During these periods, the EM fungi biomass was significantly higher in broadleaved forests. This is related to data on the species number, i.e. an average of 36 species in broadleaved forests vs. 12 species in pine forests (Table 1). Since the arbuscular mycorrhiza has not been accounted in our study, it is uncertain how much do the associated tree species, appearing in broadleaved forests (*Acer platanoides*, *Fraxinus excelsior*), affect the biomass of EM and non-EM fungi.

Conclusions

During the growing season, the soil fungi biomass in the two studied forest types changed significantly, along with fluctuating environmental factors such as temperature and soil gravitational water content. In pine forests, the amplitude of changes of the soil fungi's total biomass was lower than in broadleaved forests. The total biomass did not have significant differences in the early and late growing season (i.e. in the periods from May to July and from September to November). However, in the period from July to September, the biomass of soil fungi in broadleaved forests was noticeably higher, which completely coincides with the period of the highest soil humidity there.

In both forest types, the non-EM fungi biomass dynamics was closely correlated to the gravitational soil water content, being higher during periods with a higher humidity. In pine forests, the non-EM fungi biomass was higher than in broadleaved forests during periods with the total less throughfall due to the better moisture retention capabilities of the litter. During the periods with the highest precipitation, the non-EM fungi biomass in broadleaved forests exceeded values of this parameter in pine forests by 2.5 times. During the growing season, no clear effect of the average temperature on the non-EM fungi biomass was found. In broadleaved forests, a significant decrease in their biomass was noted from September to November, where the average temperature decreased. However, it was also the period, when the highest amplitude of daily temperatures was observed, which could

also play its role in the found changes. The EM fungi biomass dynamics did not correlate directly with humidity or temperature fluctuations, having a different nature in the studied forest types and presumably depending mainly on nutrient inputs and vegetative activity of plants.

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References

- Allen M.F. 2007. Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose Zone Journal* 6(2): 291–297. DOI: 10.2136/vzj2006.0068
- Allen M.F., Kitajima K. 2014. Net primary production of ectomycorrhizas in a California forest. *Fungal Ecology* 10: 81–90. DOI: 10.1016/j.funeco.2014.01.007
- Allison S.D., Treseder K.K. 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology* 14(12): 2898–2909. DOI: 10.1111/j.1365-2486.2008.01716.x
- Anderson J.P.E., Domsch K.H. 1975. Measurement of bacterial and fungal contributions to respiration of selected agricultural and forest soils. *Canadian Journal of Microbiology* 21(3): 314–322. DOI: 10.1139/m75-045
- Bahr A., Ellström M., Akselsson C., Ekblad A., Mikusinska A., Wallander H. 2013. Growth of ectomycorrhizal fungal mycelium along a Norway spruce forest nitrogen deposition gradient and its effect on nitrogen leakage. *Soil Biology and Biochemistry* 59: 38–48. DOI: 10.1016/j.soilbio.2013.01.004
- Boddy L. 1993. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycological Research* 97(6): 641–655. DOI: 10.1016/S0953-7562(09)80141-X
- Booth M.G. 2004. Mycorrhizal networks mediate overstorey-understorey competition in a temperate forest. *Ecology Letters* 7(7): 538–546. DOI: 10.1111/j.1461-0248.2004.00605.x
- Braun-Blanquet J. 1964. *Pflanzensociologie*. Vienna: Springer Vienna. 865 p.
- Brundrett M.C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* 154(2): 275–304. DOI: 10.1046/j.1469-8137.2002.00397.x
- Cairney J.W. 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. *Soil Biology and Biochemistry* 47: 198–208. DOI: 10.1016/j.soilbio.2011.12.029
- Carteron A., Beigas M., Joly S., Turner B.L., Laliberté E. 2021. Temperate forests dominated by arbuscular or ectomycorrhizal fungi are characterized by strong shifts from saprotrophic to mycorrhizal fungi with increasing soil depth. *Microbial Ecology* 82(2): 377–390. DOI: 10.1007/s00248-020-01540-7
- Clemmensen K.E., Bahr A., Ovaskainen O., Dahlberg A., Ekblad A., Wallander H., Stenlid J., Finlay R.D., Wardle D.A., Lindahl B. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339(6127): 1615–1618. DOI: 10.1126/science.1231923
- Compant S., van der Heijden M.G.A., Sessitsch A. 2010. Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiology Ecology* 73(2): 197–214. DOI: 10.1111/j.1574-6941.2010.00900.x
- Cornelissen J., Aerts R., Cerabolini B., Werger M., van der Heijden M. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* 129(4): 611–619. DOI: 10.1007/s004420100752
- Craig M.E., Turner B.L., Liang C., Clay K., Johnson D.J., Phillips R.P. 2018. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Global Change Biology* 24(8): 3317–3330. DOI: 10.1111/gcb.14132
- Derome J., Nieminen T. 1998. Metal and macronutrient fluxes in heavy-metal polluted Scots pine ecosystems in SW Finland. *Environmental Pollution* 103(2–3): 219–228. DOI: 10.1016/S0269-7491(98)00118-3
- Fisher F.M., Gosz J.R. 1986. Effects of trenching on soil processes and properties in a New Mexico mixed-conifer forest. *Biology and Fertility of Soils* 2(1): 35–42. DOI: 10.1007/BF00638959
- Futai K., Taniguchi T., Kataoka R. 2008. Ectomycorrhizae and Their Importance in Forest Ecosystems. In: Z.A. Siddiqui, M.S. Akhtar, K. Futai (Eds.): *Mycorrhizae: sustainable agriculture and forestry*. Dordrecht: Springer. P. 241–285. DOI: 10.1007/978-1-4020-8770-7_11
- Gonthier P., Giordano L., Zampieri E., Lione G., Vizzini A., Colpaert J.V., Balestrini R. 2019. An ectomycorrhizal symbiosis differently affects host susceptibility to two congeneric fungal pathogens. *Fungal Ecology* 39: 250–256. DOI: 10.1016/j.funeco.2018.12.008
- Gornov A.V., Gornova M.V., Tikhonova E.V., Shevchenko N.E., Kuznetsova A.I., Ruchinskaya E.V., Tebenkova D.N. 2018. Population-based assessment of succession stage of mixed forests in european part of Russia. *Russian Journal of Forest Science* 4: 243–257. DOI: 10.1134/S0024114818040083 [In Russian]
- Hawkes C.V., Kivlin S.N., Rocca J.D., Huguet V., Thomsen M.A., Suttle K.B. 2011. Fungal community responses to precipitation. *Global Change Biology* 17(4): 1637–1645. DOI: 10.1111/j.1365-2486.2010.02327.x
- Heinemeyer A., Hartley I.P., Evans S.P., Carreira de La Fuente J.A., Ineson P. 2007. Forest soil CO₂ flux: uncovering the contribution and environmental responses of ectomycorrhizas. *Global Change Biology* 13(8): 1786–1797. DOI: 10.1111/j.1365-2486.2007.01383.x

- Hendricks J.J., Mitchell R.J., Kuehn K.A., Pecot S.D. 2016. Ectomycorrhizal fungal mycelia turnover in a longleaf pine forest. *New Phytologist* 209(4): 1693–1704. DOI: 10.1111/nph.13729
- IUSS Working Group WRB. 2015. *International soil classification system for naming soils and creating legends for soil maps*. World Soil Resources Reports №106. Rome: FAO. 216 p.
- Kaisermann A., Maron P.A., Beaumelle L., Lata J.C. 2015. Fungal communities are more sensitive indicators to non-extreme soil moisture variations than bacterial communities. *Applied Soil Ecology* 86: 158–164. DOI: 10.1016/j.apsoil.2014.10.009
- Karliński L. 2021. Biomass of external mycelium of ectomycorrhizal fungi associated with poplars – The impact of tree genotype, tree age and soil environment. *Applied Soil Ecology* 160: 103847. DOI: 10.1016/j.apsoil.2020.103847
- Kazakova A.I., Semikolennykh A.A., Gornov A.V., Gornova M.V., Lukina N.V. 2018. Influence of vegetation on the lability characteristics of sandur areas of the Bryansky Les Nature Reserve. *Moscow University Soil Science Bulletin* 73(3): 100–106. DOI: 10.3103/S0147687418030055
- Keller A.B., Brzostek E.R., Craig M.E., Fisher J.B., Phillips R.P. 2021. Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type. *Ecology Letters* 24(4): 626–635. DOI: 10.1111/ele.13651
- Kernaghan G. 2005. Mycorrhizal diversity: cause and effect?. *Pedobiologia* 49(6): 511–520. DOI: 10.1016/j.pedobi.2005.05.007
- Korneykova M.V., Vasenev V.I., Nikitin D.A., Dolgikh A.V., Soshina A.S., Myazin V.A., Nakhaev M.R. 2022. Soil microbial community of urban green infrastructures in a polar city. *Urban Ecosystems* 25(5): 1399–1415. DOI: 10.1007/s11252-022-01233-8
- Korneykova M.V., Myazin V.A., Fokina N.V., Chaporgina A.A., Nikitin D.A., Dolgikh A.V. 2023. Structure of Microbial Communities and Biological Activity in Tundra Soils of the Euro-Arctic Region (Rybachy Peninsula, Russia). *Microorganisms* 11(5): 1352. DOI: 10.3390/microorganisms11051352
- Kropp B.R., Langlois C.G. 1990. Ectomycorrhizae in reforestation. *Canadian Journal of Forest Research* 20(4): 438–451. DOI: 10.1139/x90-061
- Kuznetsova A.I., Lukina N.V., Tikhonova E.V., Gornov A.V., Gornova M.V., Smirnov V.E., Geraskina A.P., Shevchenko N.E., Tebenkova D.N., Chumachenko S.I. 2019. Carbon stock in sandy and loamy soils of coniferous–broadleaved forests at different succession stages. *Eurasian Soil Science* 52(7): 756–768. DOI: 10.1134/S1064229319070081
- Laganière J., Paré D., Bergeron Y., Chen H.Y.H. 2012. The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. *Soil Biology and Biochemistry* 53: 18–27. DOI: 10.1016/j.soilbio.2012.04.024
- Lukina N.V. 2018. *Carbon accumulation and the succession status of forests*. Moscow: KMK Scientific Press Ltd. 232 p. [In Russian]
- Nikitin D.A., Chernov T.V., Zhelezova A.D., Tkhakakhova A.K., Nikitina S.A., Semenov M.V., Xenofontova N.A., Kutovaya O.V. 2019. Seasonal dynamics of microbial biomass in soddy-podzolic soil. *Eurasian Soil Science* 52(11): 1414–1421. DOI: 10.1134/S1064229319110073
- Nikitin D.A., Semenov M.V., Ksenofontova N.A., Tkhakakhova A.K., Rusakova I.V., Lukin S.M. 2023. Effect of Fresh Organic Matter of Straw on Microbiological Parameters of Soddy-Podzolic Soil. *Eurasian Soil Science* 56(5): 651–662. DOI: 10.1134/s1064229322601950
- Nilsson L.O., Giesler R., Bååth E., Wallander H. 2005. Growth and biomass of mycorrhizal mycelia in coniferous forests along short natural nutrient gradients. *New Phytologist* 165(2): 613–622. DOI: 10.1111/j.1469-8137.2004.01223.x
- Okada K., Okada S., Yasue K., Fukuda M., Yamada A. 2011. Six-year monitoring of pine ectomycorrhizal biomass under a temperate monsoon climate indicates significant annual fluctuations in relation to climatic factors. *Ecological Research* 26(2): 411–419. DOI: 10.1007/s11284-011-0800-0
- Osono T., Hagiwara Y., Masuya H. 2011. Effects of temperature and litter type on fungal growth and decomposition of leaf litter. *Mycoscience* 52(5): 327–332. DOI: 10.1007/S10267-011-0112-9
- Pagano M.C. 2014. Drought stress and mycorrhizal plant. In: M. Miransari (Eds.): *Use of Microbes for the Alleviation of Soil Stresses*. Vol. 1. New York: Springer. P. 97–110. DOI: 10.1007/978-1-4614-9466-9_5
- Pietikäinen J., Pettersson M., Bååth E. 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiology Ecology* 52(1): 49–58. DOI: 10.1016/j.femsec.2004.10.002
- Read D.J., Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance?. *New Phytologist* 157(3): 475–492. DOI: 10.1046/j.1469-8137.2003.00704.x
- Sato Y., Kumagai T., Kume A., Otsuki K., Ogawa S. 2004. Experimental analysis of moisture dynamics of litter layers – the effects of rainfall conditions and leaf shapes. *Hydrological Processes* 18(16): 3007–3018. DOI: 10.1002/hyp.5746
- Simard S., Austin M. 2010. The role of mycorrhizas in forest soil stability with climate change. In: S. Simard (Ed.): *Climate change and variability*. InTech (On-line). P. 275–302. DOI: 10.5772/9813
- Smith S.E., Read D.J. 2008. *Mycorrhizal Symbiosis*. London: Academic Press. 800 p.
- Söderström B.E. 1977. Vital staining of fungi in pure cultures and in soil with fluorescein diacetate. *Soil Biology and Biochemistry* 9(1): 59–63. DOI: 10.1016/0038-0717(77)90061-X
- Susyan E.A., Wirth S., Ananyeva N.D., Stolnikova E.V. 2011. Forest succession on abandoned arable soils in European Russia – Impacts on microbial biomass, fungal-bacterial ratio, and basal CO₂ respiration activity. *European Journal of Soil Biology* 47(3): 169–174. DOI: 10.1016/j.ejsobi.2011.04.002
- Štursová M., Kohout P., Human Z.R., Baldrian P. 2020. Production of fungal mycelia in a temperate coniferous forest shows distinct seasonal patterns. *Journal of Fungi* 6(4): 190. DOI: 10.3390/jof6040190
- Valdés R.C., Mendoza-Villarreal R., García F.G., González-Morales S., Sánchez-Peña S. 2019. Improved param-

- ters of *Pinus greggii* seedling growth and health after inoculation with ectomycorrhizal fungi. *Southern Forests* 81(1): 23–30. DOI: 10.2989/20702620.2018.1474415
- Voříšková J., Brabcová V., Cajthaml T., Baldrian P. 2014. Seasonal dynamics of fungal communities in a temperate oak forest soil. *New Phytologist* 201(1): 269–278. DOI: 10.1111/nph.12481
- Wallander H., Nilsson L.O., Hagerberg D., Bååth E. 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytologist* 151(3): 753–760. DOI: 10.1046/j.0028-646x.2001.00199.x
- Wang C., Fu B., Zhang L., Xu Z. 2019. Soil moisture–plant interactions: an ecohydrological review. *Journal of Soils and Sediments* 19(1): 1–9. DOI: 10.1007/s11368-018-2167-0
- Xu X.M. 1996. On estimating non-linear response of fungal development under fluctuating temperatures. *Plant Pathology* 45(2): 163–171. DOI: 10.1046/j.1365-3059.1996.d01-134.x
- Zvyagintsev D.G. 1991. *Methods of the soil microbiology and biochemistry*. Moscow: Moscow State University. 304 p. [In Russian]

СВЯЗЬ МЕЖДУ СЕЗОННОЙ ДИНАМИКОЙ ПОЧВЕННЫХ ГРИБОВ И ФАКТОРАМИ СРЕДЫ В ПРЕОБЛАДАЮЩИХ ТИПАХ ЛЕСА БРЯНСКОГО ПОЛЕСЬЯ (ЕВРОПЕЙСКАЯ РОССИЯ)

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Являясь важнейшей частью микробного пула лесной почвы, почвенные грибы в целом и микоризные грибы в частности являются важным объектом изучения, когда речь идет об устойчивости и сохранении лесных экосистем. С целью оценки сезонной динамики биомассы почвенных грибов в целом и эктомикоризных грибов в частности в течение вегетационного периода (май – ноябрь) и ее зависимости от биотических и абиотических факторов среды, таких как влажность почвы, температура и растительность, было проведено исследование в Государственном природном биосферном заповеднике «Брянский лес», расположенном в юго-восточной части Брянского полесья (Европейская Россия). Исследование проводилось в двух типах лесов: сосняках зеленомошно-кустарниковых и полидоминантных лиственно-широколиственных неморально-травных лесах с елью. Вегетационный период был разделен на три периода наблюдения: ранний (май – июль), средний (июль – сентябрь) и поздний (сентябрь – ноябрь). Метод, использованный для оценки биомассы грибов, представлял собой прямое микроскопическое наблюдение с окрашиванием образцов флуоресцеина диацетатом; для оценки биомассы эктомикоризных грибов отдельно использовали методы окапывания и сетчатых мешков. Полученные результаты свидетельствуют о том, что биомасса почвенных грибов увеличивается в обоих типах леса в течение вегетационного периода, в большей степени зависит от типа леса, количества доступной воды и сезонных изменений, в то время как влияние температуры менее выражено. В среднем биомасса почвенных грибов была выше в широколиственных лесах, при этом неэктомикоризный компонент имел сопоставимую биомассу в обоих типах. Динамика биомассы различалась в разных типах леса, однако заметные различия между ними были отмечены только в июле – сентябре. Биомасса эктомикоризных грибов была меньше, чем биомасса немикоризных грибов, но в то же время менее подвержена влиянию изменений влажности. Кроме того, исследования показали, что характеристики лесной подстилки могут существенно влиять на динамику биомассы грибов. Полученные данные могут быть полезны в дальнейших исследованиях микоризных грибов в условиях меняющегося климата.

Ключевые слова: государственный природный биосферный заповедник «Брянский лес», почвенная вода, температура, растительность, хвойно-широколиственные леса, эктомикоризные грибы